On the taxonomic status of the enigmatic Phycolepidoziaceae (Marchantiophyta: Jungermanniales) with description of a new species, Phycolepidozia indica

Gradstein, S Robbert ; Laenen, Benjamin ; Frahm, Jan-Peter ; Schwarz, Uwe ; Crandall-Stotler, Barbara J ; Engel, John J ; Von Konrat, Matthew ; Stotler, Raymond E ; Shaw, Blanka ; Shaw, A Jonathan

DOI: https://doi.org/10.12705/633.17

On the taxonomic status of the enigmatic Phycolepidoziaceae (Marchantiophyta: Jungermanniales) with description of a new species, *Phycolepidozia indica*

S. Robbert Gradstein,[1]* Benjamin Laenen,[2]* Jan-Peter Frahm,[3]† Uwe Schwarz,[4] Barbara J. Crandall-Stotler,[5] John J. Engel,[6] Matthew von Konrat,[6] Raymond E. Stotler,[5]† Blanka Shaw[7] & A. Jonathan Shaw[7]

1 *Museum National d'Histoire Naturelle, Department Systématique et Evolution, C.P. 39, 57 Rue Cuvier, 75231 Paris 05, France*
2 *Institut für Systematische Botanik, Universität Zürich, Zollikerstrasse 107, 8008 Zürich, Switzerland*
3 *Nees Institut für Biodiversität der Pflanzen, Universität Bonn, Meckenheimer Allee 170, 53111 Bonn, Germany*
4 *Prestige Grand Oak 202, 7th Main, 1st Cross, HAL IInd Stage, Indira Nagar, Bangalore 560038, India*
5 *Department of Plant Biology, Southern Illinois University, Carbondale, Illinois 62901-6509, U.S.A.*
6 *Department of Botany, The Field Museum, Chicago, Illinois 60605-2496, U.S.A.*
7 *Department of Biology, Duke University, Durham, North Carolina 27708, U.S.A.*
* contributed equally to this paper
Author for correspondence: *S. Robbert Gradstein, gradstein@mnhn.fr*

DOI http://dx.doi.org/10.12705/633.17

Abstract The monospecific Phycolepidoziaceae with the single neotropical species *Phycolepidozia exigua* is a highly specialized leafy liverwort without vegetative leaves. The extreme reduction of morphological and anatomical characters of *Phycolepidozia* has caused uncertainties as to the systematic position of the genus and family. In 2012, a second species of *Phycolepidozia* was detected in the Western Ghats, South India. The Indian plant differs from *P. exigua* in several respects and is described here as *P.* (subg. *Metaphycolepidozia*) *indica* Gradst., J.-P.Frahm & U.Schwarz. Differences include the massive stem of *P. indica*, the larger perianth with a crenate, 3-lobed mouth, and the epidermis of the capsule wall made up of non-tiered cells with nodular thickenings on both longitudinal and transverse walls. A phylogenetic analysis using four different chloroplast regions (*psbA*, *psbT*, *rps4*, *rbcL*) of *P. indica* and putatively related groups shows that *Phycolepidozia* is nested within the leafy liverwort family Cephaloziellaceae. Consequently, Phycolepidoziaceae is placed in the synonymy of Cephaloziellaceae. The discovery of *P. indica* adds a further example to the list of amphi-Pacific tropical disjunctions in bryophytes.

Keywords amphi-Pacific tropical disjunction; Cephaloziellaceae; leafless stems; liverworts; molecular phylogeny; *Phycolepidozia*; taxonomy; Western Ghats

Supplementary Material The alignment is available in the Supplementary Data section of the online version of this article at http://www.ingentaconnect.com/content/iapt/tax

■ INTRODUCTION

The genus *Phycolepidozia* R.M.Schust. (Marchantiophyta: Jungermanniales) is a unique, alga-like leafy liverwort, differing from all known liverworts by having stems and branches without leaves and underleaves but with leafy gametoecia. The genus is monospecific, containing the single species *P. exigua* R.M.Schust. from the Neotropics (Schuster, 1966). Schuster assigned *Phycolepidozia* to a separate family, Phycolepidoziaceae R.M.Schust., because its characters did not fit any other family. He considered affinities of *Phycolepidozia* to Cephaloziellaceae, Cephaloziaceae and Lepidoziaceae but excluded it from the latter two families because of the highly reduced seta consisting of only eight rows of cells (four rows of large epidermal cells surrounding four rows of minute inner cells). From Lepidoziaceae the genus differs further by the scattered rhizoids and elaters with tapered ends. By its seta structure *Phycolepidozia* is similar to Cephaloziellaceae, the reduced 4+4 seta being diagnostic of this family. Nevertheless, Schuster (1966) considered a close affinity of *Phycolepidozia* to Cephaloziellaceae "improbable" because of its very thin, leafless stems and the ciliate perianth mouth, and he suggested that the cephalozielloid seta of *Phycolepidozia* was a homoplastic character.

Phycolepidoziaceae have since been accepted as a separate family by all authors (e.g., Fulford, 1968; Crandall & al., 2009) with the exception of Gradstein & al. (2001) who united Phycolepidoziaceae with Lepidoziaceae. Its single species, *Phycolepidozia exigua*, was collected in 1966 by the late Dr. Rudolf M. Schuster on the island of Dominica where it was found growing on tree trunks in humid rainforest at ca. 450 m. Attempts to recollect *P. exigua* in the type locality, or elsewhere, have long been unsuccessful and the species has been redlisted as "Critically Endangered" (Schäfer-Verwimp, 2010; Hallingbäck, 2013). A second locality of the species (based on

Received: 29 Sep 2013 | returned for revisions: 7 Nov 2013; 27 Nov 2013; 8 Feb 2014 | revisions received: 24 Nov 2014; 16 Jan 2014; 8 Feb 2014 | accepted: 8 Feb 2014 | not published online ahead of inclusion in print and online issues

a 25-year-old herbarium specimen) has recently been discovered on Cerro Duida in the Guayana Highland of Venezuela (Gradstein, in press).

Surprisingly, a new species of *Phycolepidozia* differing from *P. exigua* in several important respects was collected by one of us (US) in the Western Ghats, South India, in November 2012. Because of the puzzling morphology of the genus and uncertainties about the status of the family Phycolepidoziaceae, we employed DNA sequences to explore its phylogenetic relationships. Several genomic regions of leafy liverworts have recently been sequenced and have given important new insights in the intricate phylogenetic relationships within this large group of plants (see Crandall-Stotler & al., 2009, for review). In this study we have employed different chloroplast DNA loci, which are very important and straight-forward sources of information for phylogenetic inference at generic and family level in liverworts (e.g., Stech & Quandt, 2010). By sequencing four chloroplastic regions of *Phycolepidozia* and comparing the recovered sequences with those of putatively related groups, we assessed the relationships of this enigmatic liverwort.

■ MATERIALS AND METHODS

Relationships of *Phycolepidozia* and of the family Phycolepidoziaceae were investigated using sequence data from the material of the new species from India. DNA was extracted using the DNeasy Plant Minikit (Qiagen Benelux B.V., Venlo, The Netherlands). Four chloroplast regions (*psbA*, *psbT*, *rps4*, *rbcL*) were amplified following the protocol described in Laenen & al. (2011). The four loci were concatenated and aligned to six accessions (genera) of the unpublished "Liverwort Tree of Life" database (LiToL; http://biology.duke.edu/bryology/LiToL/) and to 29 accessions from GenBank, using the program Seaview v.4.4.2 (Gouy & al., 2010). The additional accessions were chosen based on putative relationships of Phycolepidoziaceae (Schuster, 1966). Gaps were inserted when necessary to achieve character homology and scored as missing data. We used maximum likelihood (ML) and parsimony (MP) analysis for phylogenetic analysis of the data. Maximum likelihood analysis was performed using the program RAxML-HPC v.7.0.4 (Liu & al., 2011) on the Cipres data portal (Miller & al., 2009). A fifty percent majority-rule consensus tree was built based on one thousand bootstrap replicates using the GTRCAT model and the rapid bootstrapping option. Parsimony analysis was done using PAUPRat (Sikes & Lewis, 2001) on the Cipres data portal. Heuristic searches with 10,000 random taxon replicates were conducted with tree-bisection-reconnection (TBR) branch-swapping. Characters were equally weighted. We also conducted a bootstrap analysis with 100 replicates and 10 random starting points, using the TBR option. A consensus tree was built from the equally best trees retained during the heuristic search and compared to the ML consensus tree for detecting potential disagreement.

■ RESULTS

Description of the new species

Phycolepidozia indica Gradst., J.-P.Frahm & U.Schwarz, **sp. nov.** – Holotype: INDIA. Western Ghats, Karnataka State, Coorg District, trail to the summit of Mount Tandiandamol, 25.9 km SSW of Madikeri, 1610 m, on a shaded

Fig. 1. Habit of *Phycolepidozia indica*. — Scale: 1 cm.

rock in remnant forest along the trail, 75°36′34.20″ E, 12°13′14.68″ N, 11 Nov. 2012, *U. Schwarz, J.-P. Frahm & F. Schumm s.n.* (PC!; isotypes: LWG!, hb. Schwarz 10659!).

Morphological description (Figs. 1–2). – Autoicous. Plants forming small, bristle-like greenish mats on rock, consisting of short, creeping rhizomes giving rise to ascending leafless shoots to 8 mm long, without leaves and underleaves but with leafy gametoecia on short branches. Stems irregularly branched, pale green when young, deep green when mature, turning blackish-green when dry, up to 1 cm long, *100–140 µm in diameter, of up to ca. 200 rows of uniformly thickened cells* (*50–60 epidermal cells, 140–150 inner cells*), *stem surface straight to remotely angled, without slime papillae;* dorsal epidermal cells in surface view irregularly oblong, ca. 13–18 × 7–10 µm, thick-walled, deep green, ventral epidermal cells shorter, subquadrate, inner stem cells narrowly rectangular, pale; *stems in cross section ca. 15 cells wide, with numerous strongly and ± evenly thick-walled outer cells (in 3–4 rows) with small lumina surrounding 15–20 thinner-walled and larger inner cells.* Branches ventral-intercalary, arising at straight angles from ventral surface of stem. Leaves and underleaves lacking but leaves *sometimes indicated by a large, hyaline cell protruding from stem surface, places of leaf insertion indicated by remote crenations of stem surface*. Cuticle smooth. Oil bodies present in all green cells of male and female bracts and perianth, (1–)2–5 per cell, rounded to ellipsoid, finely papillose, *Jungermannia*-type; oil bodies

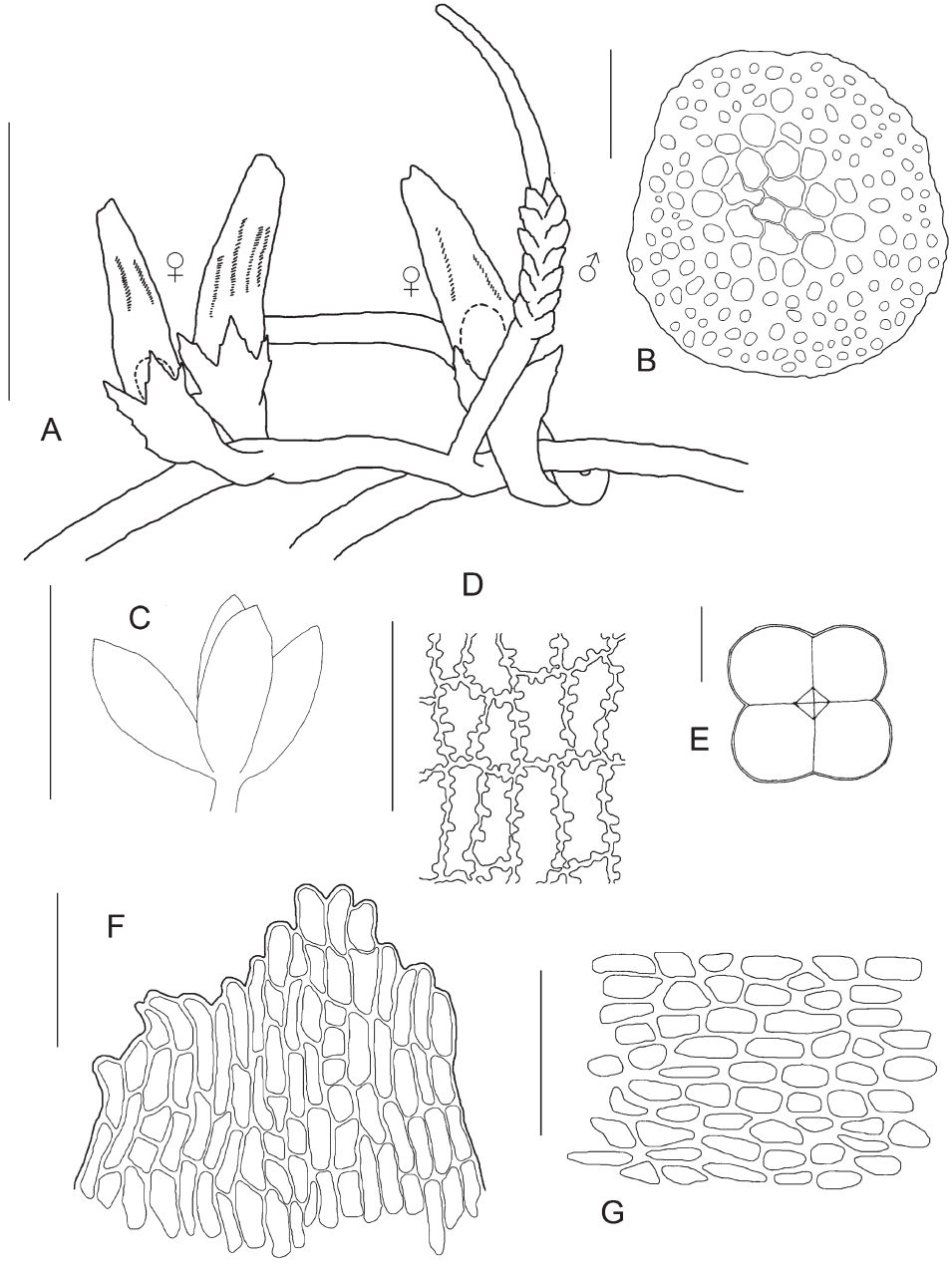

Fig. 2. *Phycolepidozia indica*. **A,** habit with gynoecia and androecia (scale: 1 mm); **B,** stem in cross section (scale: 50 µm); **C,** dehisced capsule (scale: 0.5 mm); **D,** cells of middle of inner valve surface (scale: 50 µm); **E,** seta in cross section (scale: 50 µm); **F,** cells of perianth mouth (scale: 50 µm); **G,** stem epidermis cells in surface view (scale: 50 µm).

apparently lacking in stem cells. Rhizoids hyaline to pale brown, very scarce, present on rhizomes and occasionally 1–2 near shoot tips, arising singly from ventral epidermal cells (not in bundles), on rhizomes dense and short, hyaline to pale brown, at shoot tips hyaline, elongate. Asexual reproduction not observed. Androecia terminal to intercalary (by continued growth of shoots) on main stems and short or long branches, spicate, leafy. Male bracts very small, imbricate, obliquely spreading, upper part and margins colorless, lower part green, *in 6–10 pairs, 0.2 × 0.15 mm,* bracts becoming smaller towards apex of spike, bifid to 1/3, sinus wide, V-shaped, *lobes triangular, ca. 6 cells long and 6 cells wide at base,* bluntly acute, undivided part of lamina deeply pouched, *made up of numerous non-tiered cells with evenly thickened walls,* margins subentire, bases cuneate and acutely subauriculate; bracts with one globose antheridium; antheridial stalk not seen. Male bracteoles lacking. Gynoecia colorless, on short ventral branches, with connate bracts and bracteoles. Female bracts in 2–3 series, inner bract ovate-elongate, 0.3–0.4 mm long, appressed to perianth base below, spreading above, asymmetrically bifid (to max. 1/4), lobes subacute to shortly ciliate by 1–3 elongate cells, lobe margins irregularly crenate and sometimes with a large lobe-like tooth. Female bracteoles slightly shorter and narrower than bracts, more deeply bifid (to 1/3), lobe margins subentire. Cells of bracts and bracteoles with evenly thickened walls. Perianth long-cylindrical, *1–1.3 mm long,* deeply 3-keeled, upper part colorless, *deeply 3-lobed at mouth (to 1/4 of perianth length), apical margin crenate.*

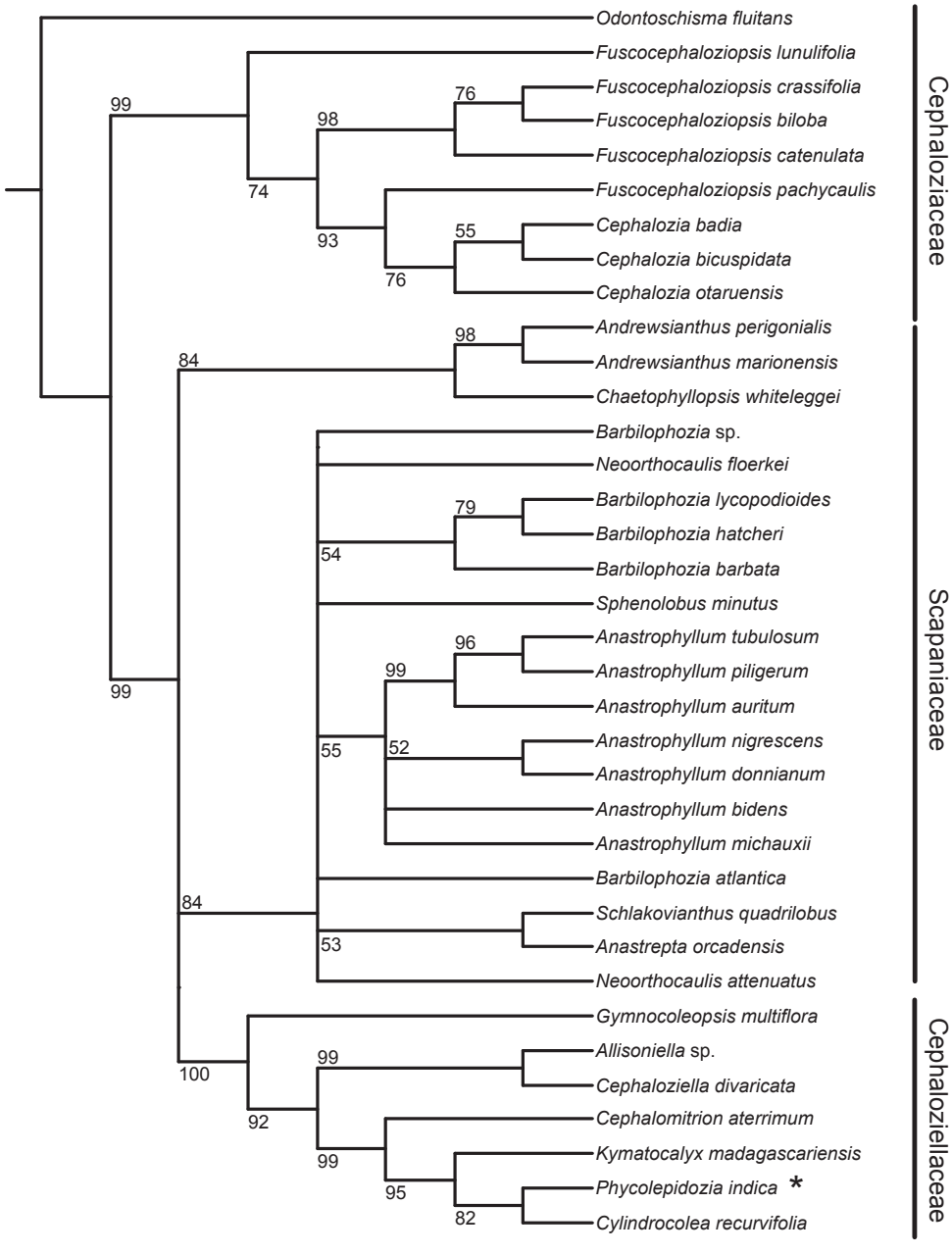

Fig. 3. Fifty percent majority-rule consensus tree based on 36 accessions using four cpDNA loci and showing the relationship among Cephaloziaceae, Scapaniaceae and Cephaloziellaceae. The position of *Phycolepidozia* is marked by an asterisk. Values on branches represent bootstrap support.

Sporophyte: Seta very thin, ca. 100–120 µm in diameter, ca. 3 mm long upon elongation, not articulate, formed of 4 rows of very large epidermal cells surrounding 4 minute rows of opposite inner cells, epidermis cells in surface view subrectangular, ca. 70 µm long and 50 µm wide, inner cells lacking towards base of seta. Capsule dark brown, ellipsoid, *0.35 × 0.25 mm,* quadrifid to near base. Valves straight, oblong-fusiform, *ca. 0.4 mm long and 0.15 mm wide, ca. 15 cells long from base to apex,* very thin, bistratose, outer layer wider than inner layer, cells of the two layers not perfectly overlapping. Valve cells *not tiered*, narrowly rectangular, becoming shorter towards apex; inner valve cells with numerous well-defined, brown, *I-shaped thickenings present on all longitudinal and transversal walls,* thickening elongate-nodular in surface view, 6–10 on long walls, 1–4 on short walls, thickenings not more pronounced on alternate walls; outer valve cells with much weaker thickenings, visible as dark brown spots in the walls and not nodular-elongate. Spores pale brown, *11–13 µm in diameter,* surface densely and finely punctate, 1-celled at dispersal. Elaters free, rather sinuous, tapered to one side, *8–10 µm wide and 180–220(–250)* µm long, with 2 brownish spirals.

Distribution and ecology. – Only known from the type locality.

Further specimens. – INDIA. Western Ghats, Karnataka, Coorg Distr., Mt. Tandiandamol, 1610 m, on shaded rocks in remnant forest along the summit trail, 30 Mar 2013, *U. Schwarz & B. Ram s.n.* (hb. Schwarz 10752); ibid., 22 Dec 2013, *U. Schwarz & S. Kumar s.n.* (hb. Schwarz 12300, 12301).

Molecular phylogeny. – The concatenation of the four loci resulted in a matrix of 2217 base pairs including 490 polymorphic sites; 289 positions were parsimony-informative. Since the MP and ML topologies did not show any major conflict, only the ML 50% majority-rule consensus tree is shown here (Fig. 3). The tree contained two major well-supported clades, one including accessions of Cephaloziaceae (bootstrap support, BS 99) and the other accessions of Cephaloziellaceae (including *Phycolepidozia indica*) and Scapaniaceae (BS 99). The latter clade comprised three main lineages in an unresolved relationship, one containing the species of Cephaloziellaceae and *Phycolepidozia indica* (BS 100) and the two other ones the members of Scapaniaceae (both BS 84). *Phycolepidozia indica* was recovered in a strongly supported Cephaloziellaceae subclade (BS 99) together with *Cephalomitrion aterrimum* (Steph.) R.M.Schust., *Cylindrocolea recurvifolia* (Steph.) Inoue and *Kymatocalyx madagascariensis* (Steph.) Gradst. & Váňa, being sister to *Cylindrocolea recurvifolia* with good support (BS 82).

■ DISCUSSION

Morphological differentiation of *Phycolepidozia indica*. — *Phycolepidozia indica* resembles *P. exigua* by having naked stems without leaves and underleaves and with leafy gametoecia, purely ventral-intercalary branching, scattered rhizoids, *Jungermannia*-type oil bodies, absence of trigones (cell walls thin or evenly thickened), small androecia intercalary on the stem with bifid bracts and no bracteoles, tristichous gynoecia on short-ventral branches with connate bracts and bracteoles, long-cylindrical and deeply 3-keeled perianths with a deeply lobed mouth, a thin seta made up of four large, non-tiered rows of outer cells and four minute inner rows, bistratose capsule valves with thickenings on all longitudinal walls, etc. (Fig. 2). In spite of these striking similarities, the two species differ morphologically in several important respects (Table 1; differences are italicized in the description). The most conspicuous difference is the massive stem of *P. indica*, which in cross section is made up of about 200 cells including numerous strongly thick-walled cells in 3–4 rows surrounding 15–20 larger and thinner-walled inner cells (Fig. 2B). In contrast, the stems of *P. exigua* are very thin, consisting of 6 rows (5 outer, 1 inner) of very thin-walled cells. Also, the epidermis cells in *P. indica* (Fig. 2G) are much smaller and much more thick-walled than those of *P. exigua*. Oil bodies are present and finely papillose in both species but in *P. exigua* they occur in stem cells (also

Table 1. Comparison of *Phycolepidozia exigua* R.M.Schust. and *P. indica* Gradst. & al.

	Phycolepidozia exigua	*Phycolepidozia indica*
Stems	50 µm in diam., of 6 rows of cells	100–140 µm in diam., of ca. 200 rows of cells
Leaf position	indicated by slime papillae	indicated by crenations on stem surface
Oil bodies	in stem cells (and in gametoecia?)	in gametoecia, not in stem cells
Male bracts	3–6 pairs	6–10 pairs
Male bract lobes	2–3 cells wide	5–6 cells wide
Male bract disc	5–6 cells in 1–2 tiers	numerous non-tiered cells
Perianth	0.4–0.5 mm long, 6-lobed, mouth longly ciliate	1–1.3 mm long, 3-lobed, mouth crenate
Capsule valves	230 µm long, of 4 rows of tiered cells	400 µm long, of 15 rows of non-tiered cells
Valve thickenings	on longitudinal walls only	on longitudinal and transverse walls
Spores	13–15 µm	11–13 µm
Elaters	135–150 µm long	180–250 µm long
Distribution	tropical America	India
Habitat	bark and soil	rock

in gametoecia?) whereas in *P. indica* they were observed in the gametoecia but not in stem cells.

Further differences are seen in the gametoecia and capsules of the two species (Table 1); many of these are quantitative, however. Thus, the male spikes of *P. indica* are longer than those of *P. exigua* and the male bracts are larger and made up of non-tiered cells (cells tiered in *P. exigua*). The perianths of *P. indica* are almost twice as long as in *P. exigua* and the mouth is 3-lobed and crenate, not 6-lobed and long-ciliate as in *P. exigua*. Furthermore, the capsules of *P. indica* are larger with valves almost twice as long as in *P. exigua*, the elaters somewhat longer and the spores slightly smaller than in *P. exigua*. A marked difference is seen in the capsule epidermis which is made up of about 15 rows of non-tiered cells in *P. indica*, with nodular thickenings occurring on both longitudinal and transverse valve walls (Fig. 2D). In *P. exigua*, the capsule epidermis is made up of only four rows of tiered cells and nodular thickenings are present only on longitudinal walls, not on transverse walls. It should be noted, however, that these characters are not always stable in leafy liverworts and may vary within species. In *Cladopodiella franscisci* (Hook.) Jörg. (Cephaloziaceae) and several species of *Cephaloziella* (Spruce) Schiffn. (Cephaloziellaceae), for example, thickenings may be present or absent on the transverse walls of the capsule epidermis, and in *Cephaloziella spinigera* R.M.Schust. the epidermal cells may be tiered or non-tiered within a single capsule (Schuster, 1974, 1980). These data suggest that the taxonomic importance of the differences in the capsule walls of the two *Phycolepidozia* species should not be overrated.

Nevertheless, the differences observed between *P. exigua* and *P. indica*, especially those in the stem and perianth mouth, indicate that the two species are morphologically rather distant to each other, and they are here therefore placed in different subgenera (see Taxonomic implications). It might even be argued that the two species are not congeneric and that *P. indica* should be given generic status. We refrain from placing *P. indica* in a separate genus, however. As shown by Vanderpoorten & al. (2012) and others, an increasingly large number of monospecific genera of liverworts, among them several highly specialized and morphologically well-defined taxa, have recently been relegated to synonymy based on molecular evidence. Without molecular study of *P. exigua*, the creation of a monospecific genus for *P. indica* would seem to be premature. Genera are convenient taxonomic vehicles for the naming of groups of species (Humphries & Linder, 2009); only in rare cases they represent single species. Given the current trend in liverwort systematics of reducing monospecific genera, we believe that description of new ones should be done with great care and be avoided unless the relationship of the respective taxon to other genera is clear. In case of *P. exigua* and *P. indica*, the latter principle does not apply. The morphological differences between the two species are considerable, however, and undoubtedly warrant placement of the two in separate subgenera.

Although vegetative leaves and underleaves are absent in *P. indica*, the position of the leaves on the stems seems to be indicated by remote crenations of the stem surface. Leaf position, whether incubous or succubous, could not be determined, however. Occasionally, a relatively large, hyaline cell is present on the crenation and this might possibly represent a rudimentary leaf. An ontogenetic study of the development of the gametophyte in this species is necessary to verify this assumption. Schuster (1966) described the presence of small, 2-celled papillae on the stem surface of *P. exigua* and tentatively interpreted these as rudimentary leaves. In *P. indica*, however, hyaline papillae were not observed.

Phylogeny of *Phycolepidozia*. — The results of the molecular analysis unequivocally show that *P. indica* is a member of the family Cephaloziellaceae. Consequently, *Phycolepidozia* and Phycolepidoziaceae are transferred to Cephaloziellaceae. Morphologically, the position of Phycolepidoziaceae in Cephaloziellaceae is strongly supported by the structure of the sporophyte, which is essentially similar in the two families and fundamentally different from that of Cephaloziaceae and Lepidoziaceae, with which Phycolepidoziaceae were also compared previously (Schuster, 1966; Gradstein & al., 2001). Typical cephalozielloid features of the sporophyte of both *P. exigua* and *P. indica* are the highly reduced seta, consisting of four rows of large epidermis cells surrounding four rows of minute inner cells, and the bistratose capsule wall with thickenings on all longitudinal walls of the epidermal cells. The 4+4 seta is unique to Cephaloziellaceae and not found in any other group of liverworts (e.g., Douin, 1914; Schuster, 1971; Crandall-Stotler & al., 2009). Bistratose capsule walls are also found in Cephaloziaceae and Lepidoziaceae but in these two families thickenings are only developed on alternate walls of the epidermis ("two-phase development" of wall thickenings; Schuster, 1984). Scapaniaceae, which is part of the same clade Cephaloziellaceae in the molecular analysis (Fig. 3), shares with the latter family the presence of thickenings on all longitudinal epidermal walls but differs fundamentally by the thicker seta and capsule wall. Thus, the cephalozielloid sporophytes of *P. exigua* and *P. indica* clearly support their position in Cephaloziellaceae and refute placement of *P. exigua* in a separate family Phycolepidoziaceae as advocated by Schuster (1966), in spite of the leafless gametophyte. Further features supporting the placement of *Phycolepidozia* in Cephaloziellaceae are the *Jungermannia*-type oil bodies, the evenly thick-walled cells of stems and gametoecia, lacking trigones, as well as the scattered rhizoids. The similarities in the sporophytes and gametophytes of the two *Phycolepidozia* species suggests that their leafless habit has resulted from a single evolutionary event and is not due to convergence. A somewhat similar situation is seen in the moss genus *Ephemeropsis* K.I.Goebel.

The present molecular results confirm the monophyly of the Cephaloziellaceae. Based on molecular analyses, Forrest & al. (2006), Heinrichs & al. (2007), Hentschel & al. (2007) and others (see also Crandall-Stotler & al., 2009) found strong evidence for Cephaloziellaceae as a robust lineage sister to, but separate from, Scapaniaceae. De Roo & al. (2007), however, resolved Cephaloziellaceae within a broadly defined Scapaniaceae, albeit with weak support. Our results show an unresolved relationship of the well-supported Cephaloziellaceae and two lineages of Scapaniaceae s.l.

The deviating morphology of *Phycolepidozia*, viz. absence of leaves and underleaves in this "leafy" liverwort, indicates, along with an increasing body of evidence, that extreme morphological transformations can obscure the phylogenetic signal present in morphological data (e.g., Heinrichs & al., 2012; Vanderpoorten & al., 2012). This may sometimes lead to dramatic differences in the generic or even familial placement of taxa. Examples from liverworts include the monospecific genus *Metzgeriopsis* K.I.Goebel from Southeast Asia characterized by a unistratose thallus (often interpreted as an enlarged protonema) with leafy sexual branches arising from thallus margins. Recent molecular analysis showed that *Metzgeriopsis* is a highly modified member of the leafy liverwort genus *Cololejeunea* (Spruce) Schiffn. (Gradstein & al., 2006). Similarly, the odd thalloid genus *Mizutania* Furuki & Z.Iwats. resembling members of Aneuraceae but with leafy bracts, was recently shown to be a member of the leafy liverwort family Calypogeiaceae (Masuzaki & al., 2010).

Among mosses several examples are known of genera with highly reduced gametophytes that were difficult to classify, for example *Buxbaumia* Hedw., *Discelium* Brid., *Ephemerum* Hampe, *Ephemeropsis*, *Micromitrium* Austin and *Viridivellus* I.G.Stone (Gradstein & Wilson, 2008; Goffinet & al., 2011). In all these groups, the gametophyte is largely replaced by a persistent, photosynthetically active protonema. A striking example is *Ephemeropsis* with *E. trentepohlioides* (Renner) Sainsbury in New Zealand and Tasmania and *E. tjibodensis* K.I.Goebel in Southeast Asia, North Australia and New Caledonia. Like *Phycolepidozia*, *Ephemeropsis* was long placed in a separate family, Ephemeropsidaceae (= Nemataceae), because of the highly modified gametophyte. The peristome and calyptra of *Ephemeropsis*, however, are similar to those of Daltoniaceae (Buck, 1988). Recent molecular analysis has confirmed that *Ephemeropsis* is a member of Daltoniaceae (Shaw & al., 2003; Ho & al., 2012). The latter study also showed that the two *Ephemeropsis* species form a monophyletic lineage, in spite of considerable morphological differences in the gametophyte and the sporophyte generation of the two (Bartlett & Iwatsuki, 1985).

Examples of leafless taxa from vascular plants which were long difficult to classify are *Cuscuta* L. and *Psilotum* Sw. *Cuscuta* is a heterotrophic flowering plant with strongly reduced leaves, no roots and with reduced chloroplasts. Its leafless habit is similar to that of the heterotrophic *Cassytha filiformis* L. (Lauraceae) from Africa and is presumably an adaptation to its parasitic life style. *Cuscuta* has alternatively been treated as a member of Convolvulaceae or as a family in its own right, Cuscutaceae. The extreme reduction of morphological and anatomical characters of *Cuscuta* has made the systematic position of the genus uncertain. Molecular evidence has shown that the genus is a highly derived member of Convolulaceae (Neyland, 2001). *Psilotum* was traditionally placed in a separate phylum, Psilophyta, and considered by some the basalmost living vascular plant although relationships to the ophioglossoid ferns had also been noted. Molecular evidence has confirmed that *Psilotum* is a fern sister to Ophioglossales and not a separate phylum (Qiu & Palmer, 1999; Pryer & al., 2001).

There are several liverwort genera with highly unusual morphologies similar to those of *Phycolepidozia*, *Metzgeriopsis* and *Mizutania* that still need study. Examples are the Amazonian *Amazoopsis* J.J.Engel & G.L.Merr. (Lepidoziaceae), *Protocephalozia* (Spruce) K.I.Goebel (Cephaloziaceae) and *Pteropsiella* Spruce (Lepidoziaceae), and *Meinungeria* Frank Müll. (Lepidoziaceae) from New Caledonia, all of which are characterized by the presence of leafy gametoecia and reduction of vegetative leaves and underleaves. Of these, *Meinungeria* superficially resembles *Phycolepidozia* by its worm-like, almost leafless stems and large, subsessile gynoecia (Müller, 2007: fig. 5). However, the presence in *Meinungeria* of vestigial underleaves (made up of 3–4 radially arranged single cells) and rhizoids originating in bundles from underleaf bases sharply separate this genus from *Phycolepidozia*. Sporophytes and androecia of *Meinungeria* are unknown. Owing to their unusual morphology, the phylogenetic relationships of *Amazoopsis*, *Meinungeria*, *Protocephalozia* and *Pteropsiella* remain unclear. Molecular phylogenetic work is necessary to determine the relationships of these unusual plants.

Distribution and ecology of *Phycolepidozia indica*. — *Phycolepidozia indica* was collected near the peak of Mt. Tandiandamol in the Western Ghats, South India. Mount Tandiandamol (1750 m) is the highest peak of the mountainous Coorg District, in the southern part of the Western Ghats. The district has a seasonal tropical climate with the monsoon season starting in June and lasting until November. Annual rainfall in the adjacent Madikeri district is up to 3500 mm with an average number of 118 rainy days per year (Pascal, 1982). Fog during morning hours in the cooler months also contributes to the precipitation. Temperatures range between 19°C and 23°C throughout the year. Geologically the area between Madikeri and Virajpet is made up of metamorphic crystalline rock (granitic gneiss). Suitable rock habitats for bryophytes are mountain cliffs, river banks and sides of tracks. The forest of the summit area of Mt. Tadiandamol is dense and evergreen and has been classified as *Schefflera–Gordonia obtusa–Meliosma* forest (Pascal, 1986). The predominant tree species are *Cinnamomum verum*, *Gordonia obtusa*, *Litsea stocksii*, *Meliosma simplicifolia* subsp. *pungens*, *Neolitsea zeylanica*, *Phoebe wighti*, *Schefflera micrantha*, *Syzygium caryophyllatum* and *S. hemisphericum*.

Bryological exploration of the Western Ghats has a long history, dating back to the 19th century, and the area is being considered a hotspot of biodiversity (Gunawardene & al., 2007). Nevertheless, most bryophyte collecting has been done in parts of the Ghats further to the south, belonging to the states of Kerala and Tamil Nadu. Locations such as the Nilghiri Mts., Palni Hills and Kodaikanal are famous for their richness in species and are the type localities for many species of bryophytes (Manju & al., 2008; Daniels, 2010). In contrast, the adjacent parts of the Western Ghats belonging to the state of Karnataka remain largely unexplored (Frahm & al., 2013). Mount Tandiandamol was visited by L.T. Walker in 1897–98, who collected only moss species (see list in Brotherus, 1899). Records of liverworts from the area are few (Alam, 2012; Verma, 2009), but a comprehensive checklist of liverworts of the Coorg District does not exist.

Currently, the mountain slopes of Mt. Tandiandamol are heavily deforested and the natural vegetation is largely replaced by coffee plantations up to 1200 m and by open grassland with bushes between 1200–1750 m. Some small patches of forest remain in ravines and along the summit trail at 1600–1700 m. *Phycolepidozia indica* was found on metamorphic crystalline rock in remnant forest along the summit trail, and was quite conspicuous in the field by its naked, leafless stems with numerous gametoecia (Fig. 1). Associated bryophyte species were the mosses *Fissidens* sp., *Dixonia orientalis* (Mitt.) H.Akiy. & Tsubota and *Thamniopsis utacamundiana* (Mont.) W.R.Buck; no other liverwort species were seen growing associated with *P. indica*. Upon its discovery in November 2012 the species was found on a single rock, but during a revisit of the type locality in December 2013 the species was seen on six further rocks within the forest patch. Possibly, the species has been widespread in the area in the past but has become scarce following deforestation of the slopes of Mt. Tandiandamol.

Biogeography of *Phycolepidozia*. — The disjunct occurrence of *Phycolepidozia* in the Neotropics and in southern India is intriguing. Thorne (1972) referred to these tropical Asian-Neotropics ranges as amphi-Pacific tropical disjunctions and enumerated 89 genera of flowering plants exhibiting this type of distribution. Past migration via the North Atlantic bridges followed by local extinction and long-range dispersal have been used most commonly to explain these amphi-Pacific disjunctions, but only few examples have been analysed with molecular phylogenetic and biogeographic methods (Li & Wen, 2013).

Among bryophytes, amphi-Pacific tropical disjunctions occur in 16 genera, 7 of mosses and 9 of liverworts (Table 2). The list does not claim to be exhaustive and more bryophyte taxa exhibiting this type of distribution may exist. The amphi-Pacific tropical disjuncts occur in different habitats such as on tree trunks (*Elmerobryum*, *Mniomalia*, *Sorapilla*, *Pictolejeunea*, *Spruceanthus*, *Vitalianthus*), rock (*Cololejeunea* subg. *Chlorolejeunea*, *Ganguleea*, *Hymenostyliella*, *Luisierella*, *Myriocoleopsis*), rotten logs or soil (*Lobatiriccardia*), living leaves (*Cololejeunea* subg. *Chlorolejeunea*, *Drepanolejeunea* subg. *Rhaphidolejeunea*) and on twigs and branches in the outer canopy of the rainforest (*Ceratolejeunea grandiloba*, *Rectolejeunea*). Dispersal scenarios rather than geographical vicariance have usually been proposed by recent authors as the preferred explanations for the intercontinental ranges of bryophyte species and genera (Heinrichs & al., 2009; Gradstein, 2013b). However, most of the amphi-Pacific tropical disjuncts with the exception of *Cololejeunea* subg. *Chlorolejeunea*, *Myriocoleopsis*, *Lobatiriccardia* and *Vitalianthus* have not been analysed by molecular phylogenetic methods, and their taxonomic circumscriptions are largely based on morphology.

To better understand their biogeographic histories, the taxonomic status and distribution of these disjuncts need to be analysed by robust methods. For example, phylogenetic analysis of the putatively Asian-Neotropical *Echinocolea* R.M.Schust.

Table 2. Amphi-Pacific tropical disjunctions in bryophytes.

Taxon	No. of species	Distribution	Reference
Mosses			
Austinia Müll.Hall.	2	SE Asia, Neotropics	Buck & Crum, 1978; Gradstein & al., 2001
Elmeriobryum Broth.	3	SE Asia, C America	Buck & Tan, 2007
Ganguleea R.H.Zander	1	Himalayas, SE Brazil	Zander, 1993
Hymenostyliella Bartr.	3	SE Asia, Brazil	Zander, 1993
Luisierella Thér. & P.Varde	1	Japan, Java, Neotropics	Zander, 1993
Mniomalia Müll.Hal.	2	SE Asia, Neotropics	Norris & Koponen, 1987
Sorapilla Mitt. & Spruce	2	E Malesia, N Australia, Ecuador	Norris & Koponen, 1987
Liverworts			
Ceratolejeunea grandiloba J.B.Jack & Steph.	1 (2 subsp.)	Java, tropical Andes	Gradstein, 2013a
Cololejeunea subg. *Chlorolejeunea* Benedix	2	SE Asia, Ecuador	Gradstein & al., 2011
Drepanolejeunea subg. *Rhaphidolejeunea* (Herzog) Grolle & R.L.Zhu	11	SE Asia, Amazonia	Grolle & Zhu, 2000
Lobatiriccardia (Mizut. & S.Hatt.) Furuki	8	SE Asia, Australasia, Ecuador	Preußing & al., 2010; Nebel & al., 2013
Myriocoleopsis Schiffn.	3	Vietnam, SE Brazil, Ecuador	Pócs, 2010
Phycolepidozia R.M.Schust.	2	India, Neotropics	this paper
Pictolejeunea Grolle	6	Borneo, Neotropics	Grolle, 1977; Pócs, 2007
Rectolejeunea A.Evans	5	N Australia, Neotropics	Reiner-Drehwald & Grolle, 2012
Spruceanthus Verd.	9	SE Asia, Australia, Ecuador, Europe (†)	Grolle, 1985; Gradstein & al., 2001, 2002
Vitalianthus R.M.Schust. & Giancotti	2	China, Brazil	Wei & al., 2013

showed that the genus is nested in *Lejeunea* Lib. and may not be monophyletic (Ilkiu-Borges, 2005; but see Heinrichs & al., 2013). Similarly, the circumscriptions of the amphi-Pacific genera *Myriocoleopsis*, *Spruceanthus* and *Vitalianthus* have become questionable based on recent molecular studies (Wilson & al., 2007; Yu & al., 2013; R.L. Zhu, pers. com.). On the other hand, it should be taken into account that the disjunct amphi-Pacific ranges may reflect insufficient collecting. The moss genus *Campylopodiella* Card., for example, was long known only from the Neotropics and the Himalayan region and considered an amphi-Pacific disjunct, but was recently detected in Africa (Townsend, 2009). Undercollecting is likely in the case of *Phycolepidozia* due to its minute size. It may also hold for the epiphyllous *Drepanolejeunea* subg. *Rhaphidolejeunea*, the rheophytic *Cololejeunea* subg. *Chlorolejeunea* and *Myriocoleopsis*, and the canopy specialists *Ceratolejeunea grandiloba* and *Rectolejeunea*, all of which grow in habitats that have been little inventoried. More intensive exploration of their habitats may reveal additional localities for these intriguing amphi-Pacific taxa.

Taxonomic implications

Cephaloziellaceae Douin in Mém. Soc. Bot. France 29: 1. 1920 – Type: *Cephaloziella* (Spruce) Schiffn.
= Phycolepidoziaceae R.M.Schust. in Bull. Torrey Bot. Club 93: 442. 1966, **syn. nov.** – Type: *Phycolepidozia* R.M.Schust.

Phycolepidozia R.M.Schust. in Bull. Torrey Bot. Club 93: 438. 1966 – Type: *P. exigua* R.M. Schust.
Contains two species, in 2 subgenera.

Phycolepidozia subg. ***Phycolepidozia***
Stem of 6 rows of cells. Male bract disc of 5–6 cells in 1–2 tiers. Perianth mouth 6-lobed, longly ciliate. Capsule valves ca. 230 µm long, of 4 rows of tiered cells; thickening present on longitudinal walls only.
Contains *P. exigua* R.M.Schust. from Dominica and Venezuela.

Phycolepidozia subg. ***Metaphycolepidozia*** Gradst., J.-P.Frahm & U.Schwarz, **subg. nov.** – Type: *P. indica* Gradst., J.-P. Frahm & U.Schwarz
Stem of ca. 200 rows of cells. Male bract disc of numerous non-tiered cells. Perianth mouth 3-lobed, crenate. Capsule valves ca. 400 µm long, of 15 rows of non-tiered cells; thickenings present on longitudinal and transverse walls.
Contains *P. indica* Gradst. & al. from South India.

■ ACKNOWLEDGEMENTS

We are grateful to the editor-in-chief of Taxon and two anonymous reviewers for constructive comments and corrections on the manuscript. The work of Benjamin Laenen was supported by a BelPD-cofund Marie Curie fellowship of the European Commission.

■ LITERATURE CITED

Alam, A. 2012. Liverwort flora of Parson's valley, Nilgiri hills (Western Ghats), South India. *Arch. Bryol.* 119: 1–20.
Bartlett, J.K. & Iwatsuki, Z. 1985. The bryophyte flora of New Zealand—Taxonomy and distribution of *Ephemeropsis trentepohliodes* and *E. tjibodensis* with a note on the ecology and distribution of *Buxbaumia novae-zelandia*. *New Zealand J. Bot.* 23: 179–182. http://dx.doi.org/10.1080/0028825X.1985.10425322
Brotherus, V.F. 1899. Report on a collection of mosses made by Dr. T.L. Walker in Coorg during the cold weather of 1897–98. *Rec. Bot. Surv. India* 1: 311–329.
Buck, W.R. 1988. Another view of familial delimitation in the Hookeriales. *J. Hattori Bot. Lab.* 64: 29–36.
Buck, W.R. & Crum, H. 1978. A re-interpretation of the Fabroniaceae with notes on selected genera. *J. Hattori Bot. Lab.* 44: 347–369.
Buck, W.R. & Tan, B.C. 2007. A review of *Elmeriobryum* (Hypnaceae). *Telopea* 12: 251–256.
Crandall-Stotler, B., Stotler, R. & Long, D. 2009. Phylogeny and classification of the Marchantiophyta. *Edinburgh J. Bot.* 66: 155–198. http://dx.doi.org/10.1017/S0960428609005393
Daniels, A.E.D. 2010. Checklist of the bryophytes of Tamil Nadu, India. *Arch. Bryol.* 65: 1–117.
De Roo, R.T., Hedderson, T.A. & Söderström, L. 2007. Molecular insights into the phylogeny of the leafy liverwort family Lophoziaceae. *Taxon* 56: 301–314.
Douin, C. 1914. Le sporogone des Céphaloziellacées. *Rev. Gén. Bot.* 25: 179–195.
Forrest, L.L., Davis, E.C., Long, D.G., Crandall-Stotler, B.J., Clark, A. & Hollingsworth, M.L. 2006. Unraveling the evolutionary history of the liverworts (Marchantiophyta)—Multiple taxa, genomes, and analyses. *Bryologist* 109: 303–334. http://dx.doi.org/10.1639/0007-2745(2006)109[303:UTEHOT]2.0.CO;2
Frahm, J.-P., Schwarz, U. & Manju, C.N. 2013. A checklist of the mosses of Karnataka, India. *Arch. Bryol.* 158: 1–15.
Fulford, M.H. 1968. Phycolepidoziaceae. Manual of the leafy Hepaticae of Latin America, Part III. *Mem. New York Bot. Gard.* 11: 382–384.
Goffinet, B., Budke, J.M. & Newman, L.C. 2011. Micromitriaceae: A new family of highly reduced mosses. *Taxon* 60: 1245–1254.
Gouy, M., Guindon, S. & Gascuel, O. 2010. SeaView Version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molec. Biol. Evol.* 27: 221–224. http://dx.doi.org/10.1093/molbev/msp259
Gradstein, S.R. 2013a. Notes on early land plants today 26. Miscellaneous new synonyms in liverworts. *Phytotaxa* 81: 3–7. http://dx.doi.org/10.11646/phytotaxa.81.1.2
Gradstein S.R. 2013b. Afro-American hepatics revisited. *Polish Bot. J.* 58: 149–177.
Gradstein, S.R. & Wilson, R. 2008. Protonemal neoteny in bryophytes. Pp. 1–11 in: Mohamed, H., Bakar, B.B., Boyce, A.N. & Lee, P.K.Y. (eds.), *Bryology in the new millenium*. Kuala Lumpur: University of Malaya.
Gradstein, S.R., Churchill, S.P. & Salazar Allen, N. 2001. Guide to the bryophytes of tropical America. *Mem. New York Bot. Gard.* 86: 1–577.
Gradstein, S.R., He, X.-L., Piippo, S. & Mizutani, M. 2002. Bryophyte flora of the Huon Peninsula, Papua New Guinea LXVIII. Lejeuneaceae subfamily Ptychanthoideae (Hepaticae). *Acta Bot. Fenn.* 174: 1–88.
Gradstein, S.R., Wilson, R., Ilkiu-Borges, A.L. & Heinrichs, J. 2006. Phylogenetic relationships and neotentic evolution of *Metzgeriopsis* (Lejeuneaceae) based on chloroplast DNA sequences and morphology. *Bot. J. Linn. Soc.* 151: 293–308. http://dx.doi.org/10.1111/j.1095-8339.2006.00531.x
Gradstein, S.R., Ilkiu-Borges, A.-L. & Vanderpoorten, A. 2011. Habitat specialization triggers the evolution of unusual morphologies:

The case of *Cololejeunea stotleriana* sp. nov. from Ecuador. *Bryologist* 114: 9–22. http://dx.doi.org/10.1639/0007-2745-114.1.9

Grolle, R. 1977. *Pictolejeunea*—eine neue Gattung der Lejeuneoideae aus der Neotropis und Borneo. *Feddes Repert.* 88: 247–256. http://dx.doi.org/10.1002/fedr.19770880402

Grolle, R. 1985. Fossil *Spruceanthus* in Europe and two other hepatics in Baltic amber. *Prace Muz. Ziemi* 37: 79–85.

Grolle, R. & Zhu, R.-L. 2000. A study of *Drepanolejeunea* subg. *Rhaphidolejeunea* (Herzog) Grolle & R.L. Zhu, stat. nov. (Hepaticae, Lejeuneaceae) in China with notes on its species elsewhere. *Nova Hedwigia* 70: 373–396.

Gunawardene, N.R., Dulip Daniels, A.E., Gunatilleke, I.A.U.N., Gunatilleke, C.V.S., Karunakaran, P.V., Geetha Nayak, K., Prasad, S., Puyravaud, P., Ramesh, B.R., Subramanian, K.A. & Vasanthy, G. 2007. A brief overview of the Western Ghats-Sri Lanka biodiversity hotspot. *Curr. Sci.* 93: 1567–1572.

Hallingbäck, T. 2013. *Phycolepidozia exigua*. In: IUCN Red List of Threatened Species. Version 2013.1. http://www.iucnredlist.org (accessed 1 Sep 2013).

Heinrichs, J., Hentschel, J., Wilson, R., Feldberg, K. & Schneider, H. 2007. Evolution of leafy liverworts (Jungermanniidae, Marchantiophyta): Estimating divergence times from chloroplast DNA sequences using penalized likelihood with integrated fossil evidence. *Taxon* 56: 31–44.

Heinrichs, J., Hentschel, J., Feldberg, K., Bombosch, A. & Schneider, H. 2009. Phylogenetic biogeography and taxonomy of disjunctly distributed bryophytes. *J. Syst. Evol.* 47: 497–508. http://dx.doi.org/10.1111/j.1759-6831.2009.00028.x

Heinrichs, J., Dong, S., Yu, Y., Schäfer-Verwimp, A., Pócs, T., Feldberg, K., Hentschel, J., Schmidt, A. & Schneider, H. 2012. A 150-year mystery solved: Transfer of the rheophytic endemic liverwort *Myriocolea irrorata* to *Colura*. *Phytotaxa* 66: 55–64.

Heinrichs, J., Dong, S., Schäfer-Verwimp, A., Pócs, T., Feldberg, K., Czumaj, A., Schmidt, A.R., Reitner, J., Renner, M.A.M., Hentschel, J., Stech, M. & Schneider, H. 2013. Molecular phylogeny of the leafy liverwort *Lejeunea* (Porellales): Evidence for a neotropical origin, uneven distribution of sexual systems and insufficient taxonomy. *PloS ONE* 8: e82547. http://dx.doi.org/10.1371/journal.pone.0082547

Hentschel, J., Paton, J.A., Schneider, H. & Heinrichs, J. 2007. Acceptance of *Liochlaena* Nees and *Solenostoma* Mitt., the systematic position of *Eremonotus* Pearson and notes on *Jungermannia* L. s.l. (Jungermanniidae) based on chloroplast DNA sequence data. *Pl. Syst. Evol.* 268: 147–157. http://dx.doi.org/10.1007/s00606-007-0549-7

Ho, B.-C., Pokorny, L., Tan, B., Frahm, J.-P., Shaw, A.J. & Quandt, D. 2012. Molecular evolution and diversification of the moss family Daltoniaceae (Hookeriales, Bryophyta) with emphasis on unraveling the phylogeny of *Distichophyllum* and its allies. *Bot. J. Linn. Soc.* 170: 157–175. http://dx.doi.org/10.1111/j.1095-8339.2012.01279.x

Humphries, A.M. & Linder, H.P. 2009. Concept versus data in delimitation of plant genera. *Taxon* 58: 1054–1074.

Ilkiu-Borges, A.L. 2005. A taxonomic revision of *Echinocolea* (Lejeuneaceae, Hepaticae). *Nova Hedwigia* 80: 45–71. http://dx.doi.org/10.1127/0029-5035/2005/0080-0045

Laenen, B., Désamoré, A., Devos, N., Shaw, A.J., González-Mancebo, J.M., Carine, M.A. & Vanderpoorten, A. 2011. Macaronesia: a source of hidden genetic diversity for post-glacial recolonization of western Europe in the leafy liverwort *Radula lindenbergiana*. *J. Biogeogr.* 38: 631–639. http://dx.doi.org/10.1111/j.1365-2699.2010.02440.x

Li, R. & Wen, J. 2013. Phylogeny and biogeography of *Dendropanax* (Araliaceae), an amphi-Pacific disjunct genus between tropical/subtropical Asia and the Neotropics. *Syst. Bot.* 38: 536–551. http://dx.doi.org/10.1600/036364413X666606

Liu, K., Linder, C.R. & Warnow, T. 2011. RAxML and FastTree: Comparing two methods for large-scale maximum likelihood phylogeny estimation. *PLoS ONE* 6: e27731. http://dx.doi.org/10.1371/journal.pone.0027731

Manju, C.N., Rajesh, K.P. & Madhusoodanan, P.V. 2008. Checklist of the bryophytes of Kerala, India. *Trop. Bryol. Res. Rep.* 7: 1–24.

Masuzaki, H., Shimamura, M., Furuki, T., Tsubota, H., Yamaguchi, T., Majid, H.M.A. & Deguchi, H. 2010. Systematic position of the enigmatic liverwort *Mizutania* (Mizutaniaceae, Marchantiophyta) inferred from molecular phylogenetic analyses. *Taxon* 59: 448–58.

Miller, M.A., Holder, M.T., Vos, R., Midford, P.E., Liebowitz, T., Chan, L., Hoover, P. & Warnow, T. 2009. The CIPRES Portals. http://www.phylo.org/sub

Müller, F. 2007. *Meinungeria mouensis* (Lepidoziaceae), a new genus and species from New Caledonia. *Bryologist* 110: 494–499. http://dx.doi.org/10.1639/0007-2745(2007)110[494:MMLANG]2.0.CO;2

Nebel, M., Söderström, L., Hagborg, L. & Konrat, M. von 2013. Notes on early land plants today 28. Transfers of some taxa to Lobatiriccardia (Aneuraceae, Marchantiophyta). *Phytotaxa* 81: 10–11. http://dx.doi.org/10.11646/phytotaxa.81.1.4

Neyland, R. 2001. A phylogeny inferred from large ribosomal subunit (26S) rDNA sequences suggests that *Cuscuta* is a derived member of Convolvulaceae. *Brittonia* 53: 108–115. http://dx.doi.org/10.1007/BF02805402

Norris, D.H. & Koponen, T. 1987. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XX. Fissidentaceae, Mitteniaceae, Phyllodrepaniaceae, Phyllogoniaceae and Sorapillaceae. *Ann. Bot. Fenn.* 24: 177–219.

Pascal, J.P. 1982. *Bioclimates of the Western Ghats*. Pondicherry: Institute Français de Pondichéry.

Pascal, J.P. 1986. *Explanatory booklet on the forest map of South India. Sheets: Belgaum-Dharwar-Panaji, Shimoga, Mercara-Mysore.* Pondicherry: Institute Français de Pondichéry.

Pócs, T. 2007. A sixth species of *Pictolejeunea* (Jungermanniopsida) from the Venezuelan Guyana. *Acta Bot. Hung.* 40: 109–119. http://dx.doi.org/10.1556/ABot.49.2007.1-2.12

Pócs, T. 2010. *Myriocoleopsis* in Southeast Asia. *Trop. Bryol.* 31: 123–125.

Preußing, M., Olsson, S., Schäfer-Verwimp, A., Wickett, N.J., Wicke, S., Quandt, D. & Nebel, M. 2010. New insights in the evolution of the liverwort family Aneuraceae (Metzgeriales, Marchantiophyta) with an emphasis on the genus *Lobatiriccardia*. *Taxon* 59: 1424–1440.

Pryer, K.M., Schneider, H., Smith, A.R., Cranfill, R., Wolf, P.G., Hunt, J.S. & Sipes, S.D. 2001. Horsetails and ferns are a monophyletic group and the closest living relatives to seed plants. *Nature* 409: 618–621. http://dx.doi.org/10.1038/35054555

Qiu, Y.-L. & Palmer, J. 1999. Phylogeny of early land plants: Insights from genes and genomes. *Trends Pl. Sci.* 4: 26–30. http://dx.doi.org/10.1016/S1360-1385(98)01361-2

Reiner-Drehwald, M.E & Grolle, R. 2012. Review of the genus *Rectolejeunea* (Lejeuneaceae, Marchantiophyta). *Nova Hedwigia* 95: 451–482. http://dx.doi.org/10.1127/0029-5035/2012/0063

Schäfer-Verwimp, A. 2010. A checklist of the liverworts and hornworts of Dominica, West Indies. *Cryptog. Bryol.* 31: 313–415.

Schuster, R.M. 1966. Studies on Hepaticae XXVIII. On *Phycolepidozia*, a new, highly reduced genus of Jungermanniales of questionable affinity. *Bull. Torrey Bot. Club* 93: 437–449. http://dx.doi.org/10.2307/2483417

Schuster, R.M. 1971. Studies on Cephaloziellaceae. *Nova Hedwigia* 22: 121–265.

Schuster, R.M. 1974. *The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian*, vol. 3. New York: Columbia University Press.

Schuster, R.M. 1980. *The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian*, vol. 4. New York: Columbia University Press.

Schuster, R.M. 1984. Comparative anatomy and morphology of the Hepaticae. Pp. 760–1070 in: Schuster, R.M. (ed.), *New manual of bryology*, vol. 2. Nichinan: The Hattori Botanical Laboratory.

Shaw, A.J., Cox, C.J., Goffinet, B., Buck, W.R. & Boles, S.B. 2003. Phylogenetic evidence of a rapid radiation of pleurocarpous mosses (Bryophyta). *Evolution* 57: 2226–2241. http://dx.doi.org/10.1111/j.0014-3820.2003.tb00235.x

Sikes, D.S. & Lewis, P.O. 2001. PAUPRat: PAUP implementation of the parsimony ratchet; beta software, version 1. Storrs: Department of Ecology and Evolutionary Biology, University of Connecticut.

Stech, M. & Quandt, D. 2010. 2000 species and five key markers: The status of molecular bryophyte systematics. *Phytotaxa* 9: 196–228.

Thorne, R.F. 1972. Major disjunctions in the geographic ranges of seed plants. *Quart. Rev. Biol.* 47: 365–411. http://dx.doi.org/10.1086/407399

Townsend, C.C. 2009. *Campylopodiella dorothyae* sp. nov., a genus and species new to Africa. *J. Bryol.* 31: 127–129. http://dx.doi.org/10.1179/174328209X427515

Vanderpoorten, A., Désamoré, A., Laenen, B. & Gradstein, S.R. 2012. Striking autapomorphic evolution in *Physotheca* J.J. Engel & Gradst. (Lophocoleaceae) blurred its actual relationships with *Leptoscyphus* Mitt. *J. Bryol.* 34: 251–256. http://dx.doi.org/10.1179/1743282012Y.0000000018

Verma, P.K. 2009. Genus *Cololejeunea* (Spruce) Schiffn. in Nilgiri Hills (Western Ghats). *Nelumbo* 51: 157–160.

Wei, Y.-M., He, Q., Gradstein, S.R., Campos, L.V. & Zhu R.-L. 2013. Notes on early land plants today. 46. Transfer of *Vitalianthus urubuensis* (Marchantiophyta: Lejeuneaceae) to *Cheilolejeunea*. *Phytotaxa* 50: 50–52. http://dx.doi.org/10.11646/phytotaxa.152.1.5

Wilson, R., Gradstein, S.R., Schneider, H. & Heinrichs, J. 2007. Unravelling the phylogeny of Lejeuneaceae (Jungermanniopsida): Evidence for four main lineages. *Molec. Phylogen. Evol.* 43: 270–282. http://dx.doi.org/10.1016/j.ympev.2006.10.017

Yu, Y., Pócs, T., Schäfer-Verwimp, A., Heinrichs, J., Zhu, R.-L. & Schneider, H. 2013. Evidence for rampant homoplasy in the phylogeny of the epiphyllous liverwort genus *Cololejeunea* (Lejeuneaceae). *Syst. Bot.* 38: 553–563. http://dx.doi.org/10.1600/036364413X670304

Zander, R. 1993. Genera of the Pottiaceae. *Bull. Buffalo Soc. Nat. Sci.* 32: 1–378.

Appendix 1. GenBank accession numbers (*pbsA*, *psbT*, *rbcL*, *rps4*) of species used in this study. LiToL number, provenance, collector(s), collection number and (herbarium) and are provided for sequences newly generated in this study.

CEPHALOZIACEAE. ***Cephalozia badia*** (Gottsche) Steph., KC184779.1, –, KC184710.1, –; ***Cephalozia bicuspidata*** (L.) Dumort., KC184781.1, –, AY462291, JF513486.1; ***Cephalozia otaruensis*** Steph., KC184781.1, –, AB476560.1, –; ***Fuscocephaloziopsis biloba*** (Herzog) Fulford, –, –, KC184712.1, –; ***Fuscocephaloziopsis catenulata*** (Huebener) Váňa & L.Söderstr., –, –, –, AY608053.1; ***Fuscocephaloziopsis crassifolia*** (Lindenb. & Gottsche) Váňa & L.Söderstr., KC184780.1, –, KC184711.1, AM398309.1; ***Fuscocephaloziopsis lunulifolia*** (Dumort.) Váňa & L.Söderstr., –, –, –, AM398315.1; ***Fuscocephaloziopsis pachycaulis*** (R.M.Schust.) Váňa & L.Söderstr., KC184782.1, –, KC184714.1, –; ***Odontoschisma fluitans*** (Nees) L.Söderstr. & Váňa, KC184789.1, –, JX305542.1, –. **CEPHALOZIELLACEAE.** ***Allisoniella*** **sp.,** FATOL788, New Zealand, *Engel & Konrat 28608* (F), KF851891, –, –, KF851429; ***Cephalomitrion aterrimum*** (Steph.) R.M.Schust., L1226, New Zealand, *Engel & Konrat 28545* (F), KF851926, –, KF852368, KF851459; ***Cephaloziella divaricata*** (Sm.) Schiffn., L1426, Czech Republic, *Sova s.n.* (DUKE), KF851965, KF852248, KF852399, KF851489; ***Cylindrocolea recurvifolia*** (Steph.) Inoue, FATOL445, Japan, *Yamaguchi s.n.* 23 Sep 2007 (F), KF851848, KF852130, KF852297, KF851399; ***Gymnocoleopsis cylindriformis*** (Mitt.) R.M.Schust. (= *G. multiflora* (Steph.) R.M.Schust.), Venezuela, *Söderström 2004/091* (BOL), –, –, –, AM398239; ***Kymatocalyx madagascariensis*** (Steph.) Gradst. & Váňa, IBC64, Madagascar, *Pocs 9446/AQ* (F), AY607990, KF852200, –, AY608111; ***Phycolepidozia indica*** Gradst. & al., S India, *Schwarz 10659* (PC), KF862486, KF895402, KF862485, KF895403. **SCAPANIACEAE.** ***Anastrepta orcadensis*** (Hook.) Schiffn., JF513391.1, JF513407.1, JF513450.1, JF513468.1; ***Anastrophyllum auritum*** (Lehm.) Steph., KC184771.1, –, KC184702.1, –; ***Anastrophyllum bidens*** (Reinw. & al.) Steph., KC184769.1, –, KC184700.1, –; ***Anastrophyllum donnianum*** (Hook.) Steph., KC184770.1, –, KC184701.1, –; ***Anastrophyllum michauxii*** (F.Weber) A.Evans, –, –, AY507390.1, AY507433.1; ***Anastrophyllum nigrescens*** (Mitt.) Steph., KC184772.1, –, KC184703.1, –; ***Anastrophyllum piligerum*** (Reinw. & al.) Steph., KC184773.1, –, KC184704.1, –; ***Anastrophyllum tubulosum*** (Nees) Grolle, KC184774.1, –, KC184705.1, –; ***Andrewsianthus marionensis*** (S.W.Arnell) Grolle, KC184775.1, –, KC184706.1; ***Andrewsianthus perigonialis*** (Hook.f. & Taylor) R.M.Schust., KC184776.1, –, KC184707.1, –; ***Barbilophozia atlantica*** (Kaal.) Müll.Frib., –, –, –, AM398349.1; ***Barbilophozia barbata*** (Schreb.) Loeske, AM396187, –, JX305536.1, AM398313; ***Barbilophozia hatcheri*** (A.Evans) Loeske, KC184777.1, –, DQ312478.1, AM398338.1; ***Barbilophozia lycopodioides*** (Wallr.) Loeske, KC184778.1, –, KC297121.1, AM398333.1; ***Barbilophozia*** **sp.,** –, –, JX305573.1, JX308594.1; ***Chaetophyllopsis whiteleggei*** (Carringt. & Pears.) Hamlin, –, –, AY462292.1, AY462346.1; ***Neoorthocalis attenuatus*** (Mart.) L.Söderstr. & al., –, –, GU373417.1, –; ***Neoorthocaulis floerkei*** (Web. & Mohr) L.Söderstr. & al., –, –, KC297118.1, –; ***Schljakovianthus quadrilobus*** (Lindb.) Konstant. & Vilnet, –, –, –, AM398324.1; ***Sphenolobus minutus*** (Schreb.) Berggr., –, –, DQ312475.1, JX308554.1.